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GENETICS OF A ROLLED-LEAF MUTANT IN SMOOTH BROMEGRASS, BROMUS INERMIS LEYSS

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ABSTRACT

GENETICS OF A ROLLED-LEAF MUTANT IN SMOOTH BROMEGRASS, *BROMUS INERMIS* LEYSS

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The genetics of a rolled-leaf mutant in smooth bromegrass, *Bromus inermis* Leyss., was investigated at the octoploid level. The objective of this study was to provide information on the inheritance of the gene in the species.

Rolled-leaf mutants were observed among self-fertilized progenies of plant number 22448. The mutant character is manifested very early in seedling growth. The leaf blades roll inward from the leaf margins toward the midvein to a varying extent. The study was conducted in the field and greenhouse. Segregation data were obtained on seedlings in the greenhouse. The expression of mutant characteristics in the seedling stage was unaffected by temperature or photoperiod. Somatic chromosome counts were made on root-tips of the parents and some of the F_1 plants.

The parents and F_1 plants had predominantly 56 chromosomes. The phenotypically normal plant number 22448 segregated in the ratio of 4.6 normal : 1 rolled. F_1 plants segregated in the ratios ranging from 6 : 1 to 851 normal : 1 rolled. The genetic data from BC_1, self of BC_1, F_2, and F_3 segregation support a mode of a simple tetrasomic inheritance with differential transmission of the homozygous recessive gametes between seed and pollen parents, and incomplete dominance requiring at least two doses of the dominant allele to suppress expression of the recessive. The incompletely dominant normal allele of the rolled-leaf gene was represented by the symbol "R", and the recessive mutant allele by the symbol "r". Therefore, a phenotypically rolled-leaf mutant would be Rrrr or rrrr, and a phenotypically normal plant would be RRRR, RRRr or RRrr. Possible explanations were presented for the rare segregant, surplus recessives, and reciprocal differences in segregation ratios.

INTRODUCTION

Smooth bromegrass, Bromus inermis Leyss., is classified under the family Gramineae, sub-family Festucoidae, tribe Festuceae and the genus Bromus (18). This cultivated forage species is cross-pollinated, rhizomatous, and a sod former with abundant vegetative growth. Lack of suitable gene markers, high chromosome number ($2n = 8x = 56$), self- and cross-incompatibilities, and rapid inbreeding depression associated with high seedling mortality have all discouraged genetic work with the species.

The rolled-leaf mutant (Fig. 1) was observed in a F_2 population between a normal green plant and the temperature-sensitive albino mutant in 1971 (8). A similar mutant had occurred in a genetic nursery at University of New Hampshire Agronomy Research Farm, Madbury, New Hampshire, U.S.A. in 1961. The objective of this study was to investigate the inheritance of this mutant and the cytology of the parents and some of their F_1 progenies.

REVIEW OF LITERATURE

Genetics of Polyploids

Theories

Random Chromosome Segregation (RCS). Muller (27) reviewed the early findings of an autotetraploid segregation in Primula sinensis by Gregory (13). Gregory assumed allosyndetic pairings of homologous chromosomes in autotetraploids which gave the duplicator factor ratios of diploid species. Muller's theory assumed random assortment of any two of the four homologous chromosomes. The gametic ratio of a duplex plant (AAaa) is 1AA : 4Aa : 1aa. Upon selfing and backcrossing of a duplex to a homozygous recessive, it should give a 35A : 1a and 5A : 1a ratio, respectively, if one dominant allele produces the dominant phenotype. These expected ratios in autotetraploids suggested by Muller are known as random chromosome segregation (RCS).

Random Chromatid Segregation (RDS). Haldane (14) presented mathematical formulae which are generalized to give expected ratios for all types of polyploids. His theory assumed random assortment of chromatids without

cytological considerations for gametic formation. An autotetraploid duplex hybrid (AAaa) should give a gametic ratio of 3AA : 8Aa : 3aa. If one dominant allele is sufficient to express the dominant phenotype, the zygotic ratios expected are 20.8A : 1a and 3.7A : 1a upon selfing and backcrossing, respectively. These ratios characterize random chromatid segregation (RDS).

Maximum Equational Segregation (MES). Mather (25) proposed an involvement of meiotic events in chromatid assortment during gametogenesis of autotetraploids. He presented a formula to calculate the index alpha, (α), to represent the frequency of double reduction. Double reduction is a mechanism whereby a gamete is produced with sister chromatids. The frequency of double reduction depends upon the frequency of quadrivalent formation and crossing over between the gene and the centromere. Consequently, the gametic ratio is variable according to the type of chromosome pairing and the location of the gene on the chromosome. The maximum value of α is 1/6 and the minimum is 0. When α is 1/6, the gametic ratio of a duplex is 2AA : 5Aa : 2aa. Upon selfing and backcrossing, this produces zygotic ratios of 19.25A : 1a and 3.5A : 1a, respectively, if dominance is complete.

When α is 0, the gametic ratio of a duplex is the same as for RCS by Muller (27). These ratios are known as maximum equational segregation (MES).

Burnham (5) illustrated concisely the derivation of the expected gametic ratios in a tetrasome following Mather's MES theory, when α is maximum. He excluded RDS by Haldane from one of the theoretical extreme ratios in tetrasomic segregation because it did not give the maximum value for the double reductional gamete. The weakness of RDS theory came from overlooking some of meiotic events in gametogenesis. However, RDS presents the method to obtain close estimates of expected ratios for higher than tetraploid, while MES is effective only for the tetraploids. Burnham also summarized the cytological events necessary for double reduction at a given locus as follows; 1) quadrivalent formation, 2) crossing over between the gene and the centromere, 3) the two pairs of chromatids involved in such crossing over must pass to the same pole in anaphase I, 4) random separation of the chromatids at anaphase II.

Genetic Data in Bromus inermis

Yellow Chlorophyll-deficient Mutant. Ghosh and Knowles (12) investigated the inheritance of a dominant chlorophyll-deficient mutant (Y_1) and found that tetrasomic

inheritance was most likely for this character. They applied RCS for the lower extreme frequency of recessive individuals and RDS for the higher extreme to test their observed ratios for goodness-of-fit. They stated that "Segregations indicated chromosome segregation..... but chromatid segregation could not be excluded." Such a conclusion probably came from overlooking the facts that genetic data for tetrasomic inheritance would fall between the two extreme ratios. Mather (26) emphasized that "Unlike the diploid there is no segregation characteristic of an autotetraploid, but each gene will have its own segregation which may not be constant, since crossing-over is affected by environment." In other words, a change of genetic backgrounds and/or environment could have changed the frequency of double reduction, possibly through variations in the frequencies of quadrivalent and crossing-over in each cross or self. Little (24) summarized as follows:

> The important statistical problem is, therefore, not to determine which ratio the data fit more closely, but to find out to what extent the two opposing forces of reductional and equational separation have affected the data. Mather's index, α , conveniently characterizes a set of data in this regard.

It can be deduced from the above two citations by Mather and Little that a X^2-test of a certain genetic data against

any one of two extreme ratios is meaningless within the range of two extreme limits. Therefore, the X^2-test for goodness-of-fit should be employed only for the genetic data which exceed the range of two extreme limits against the nearest theoretical extreme ratio. For example, no X^2-test is necessary for an obtained ratio of 25 : 1 from a self of a tetrasomic duplex, but a ratio of 17 : 1 would be tested against 19.25 : 1 and a ratio of 46 : 1 would be tested against the extreme theoretical ratio of 35 : 1. Possibly for that reason, Burnham (5) rearranged genetic data from early works on tetraploid Datura by Blakeslee et. al. (4), using expected percent recessives for each theoretical extreme ratio instead of the result of X^2-test.

Temperature-sensitive Albino Mutant. Another report on tetrasomic inheritance in smooth bromegrass was given by Dunn and Nasiruddin (8) for a recessive temperature-sensitive albino mutant. The genetic data from F_2, F_3, and testcross progenies supported tetrasomic segregation for a single gene with a few exceptions. Those exceptions were three F_1 plants which did not segregate in F_2 but segregated 33 green : 1 albino, 148 : 1, and 189 : 1 in backcrosses, respectively, instead of 3.5 to 5 : 1. They suggested a variable extent of preferential

pairing between homologous chromosomes to explain these exceptions.

Cytology

Chromosome Complements

Bromus inermis is normally an octoploid with 2n = 8x = 56 (9, 17, 22, 29). Three other chromosome races from natural collections are tetraploid (2n = 4x = 28) (10,30), hexaploid (2n = 6x = 42) (22), and decaploid (2n = 10x = 70) (29). The cross-compatibility between chromosome races made it possible to produce a series of chromosome races for genome analysis and theoretical interest. However, the octoploid is the most prevalent chromosome race in a natural habitat, and is used exclusively in agriculture. Aneuploid plants with reduced seed set are common in the octoploids (15, 34). No complete karyotype has yet been established at the octoploid level for the species.

Genomic Constitution

Meiotic chromosome pairing, frequencies of micronuclei, fertility relations of intra- and inter-specific hybrids, and the number and morphology of satellite

chromosomes have been the main cytogenetic tools to determine the genomic constitution of smooth bromegrass. Also, genetic data are useful in genome analysis. Tetrasomic inheritance has been demonstrated in the genetic studies on chlorophyll mutants (8, 12), indicating there is at least one genome in tetrasomic condition. The autoalloploid nature of the species was observed in a study of the meiotic behavior of tetraploid, hexaploid hybrids, and derived octoploid progenies from a cross between a polyhaploid (2n = 4x = 28) and an octoploid (2n = 8x = 56) (7, 16). It was concluded that octoploid B. inermis is an autoallopolyploid with a genomic formula of AAAABBBB. The conclusions were primarily based on higher univalent frequencies in hexaploid hybrids compared to tetraploids and octoploids, and on normal frequencies of micronuclei in quartets of the F_1 octoploids between derived octoploid and normal octoploid. Armstrong (3) studied meiotic chromosome pairing of B. erectus (2n = 28), B. inermis (2n = 56), and interspecific hybrids from B. erectus x B. inermis (2n = 42). His results supported the two genomic formula AAAABBBB proposed by Hill and Carnahan (16), since chromosome pairing in the hybrids was complete and the quadrivalent frequency in the parents and hybrids was similar.

There are, however, several observations which are not completely in accordance with the conclusion that B. inermis is AAAABBBB. First, two pairs of chromosomes with a large satellite and one pair with a minute satellite were reported in B. inermis (12, 33), suggesting that there must be at least three different genomes in B. inermis, AAAABBCC. These observations on the number of satellite chromosomes were confirmed in a study on chromosome pairing in hexaploid hybrids between B. erectus (2n = 28) and B. inermis (2n = 56) by Armstrong (3). He suggested that a genome structurally homologous to the B. erectus genome is present in B. inermis in a tetrasomic condition, since four large satellites are also found in B. erectus. He suggested, however, that the number of satellites might not always be a good indication of the nature of polyploidy, since the number that can be found in different material in the species is variable depending upon the activity of the nucleolus organizer (20). Second, the quadrivalent frequency reported (3, 9) suggests that only one genome is in tetrasomic condition. Third, Armstrong (2) inferred that B. inermis might be AAAABBCC because of the sterility of polyhaploids of B. inermis studied by Nielsen (30), which Armstrong speculated to be AABC. In his later study, however, Armstrong favored the two

genomic formula.

Rolled-leaf Mutants

Morphological mutations with leaf rolling characteristics similar to the rolled-leaf mutant in smooth bromegrass were summarized for rice (1) and corn (11).

Jones (19) described a rolled-leaf mutant in rice which was comparatively short and partly sterile. The leaves were rather narrow and folded inward. This mutant was a simple recessive to the normal type of plant.

Mutations of this sort were described in the following independent studies in corn. Carver (7) found a semi-lethal seedling type "rolled" in maize. A rolled seedling looked normal until the third leaf emerged. With the appearance of the third leaf, all three leaves became pale, slightly corrugated cross-wise, thickened and rolled upward at the borders. At this stage all three leaves died in extreme types and fell from the plant. Some plants recovered and could not be distinguished from the normal if the growing conditions were favorable. Although some recovered so quickly that they escaped notice, the genetically rolled plants were obviously weak. This rolled character was found to be a simple Mendelian recessive.

Kempton (21) reported a mutation, "adherence", in maize. Any or all leaves, bracts, and inflorescences adhered to one another to a varying extent in this mutation. In extreme cases the upper leaves and inflorescences were so firmly compacted that the parts could not be separated. In less extreme cases the pressure of the growing parts naturally separated the adhering organs. Unless the leaves of the young plants adhered so firmly as to prevent further growth, the plants recovered and grew normally until the ear bearing node was reached, at which stage their adherent characteristics reappeared. Many of the extreme mutants died after the production of 3 to 4 leaves, and all were impossible to propagate. The progenies were obtained mostly from plants with intermediate expression. The frequency of mutants was below that expected for a simple Mendelian character. Kempton speculated that this deficiency was probably due to the mortality in the seedling stage of the most extreme adherent plants. However, he assumed that adherence is a simple Mendelian recessive.

Kvakan (23) presented the results of experiments with three genetically different "twisted" seedling types in maize. Mutant seedlings showed a pronounced twisting of the first leaves. Subsequent leaves attached to each other and failed to unfold normally, forming a more or

less defined loop. In most cases the loop opened spontaneously, and the new leaves developed normally so that mutant plants were eventually indistinguishable from normal plants. The mutants exhibited great variability. In extreme cases some of the plants never recovered and perished early, while in less severe cases the plants recovered completely. Kvakan concluded that the mutants were inherited as simple Mendelian recessives.

The mechanism leading to these morphological contortions is not known in any of these mutants. They all vary considerably in expression of the trait.

MATERIALS AND METHODS

Plant Materials

A rolled-leaf mutant (Fig. 1) was observed among self-fertilized progenies of plant number 22448 (#22448) in 1971. Plant 22448 was an F_1 between a normal green #1624 and the albino mutant #9723 (8). Plant #1624 was selected from progenies of the experimental strain PL 47-45. Plant #9723 was found in a self-pollinated population derived from the experimental line NY 46-116. Three plants, #9814, #24135, and #24251 were used as normal parents in crosses with mutants to produce F_1 plants. Plant #9814 was derived from self-progenies of the experimental strain Wisc 2-7. Plant #24135 and #24251 were selected from the commercial cultivars "Polar" and "Manchar", respectively. The normal parents were selected for high self- and cross-fertility to provide high self-fertility in the later generations. The mutant parent population was established by selection of mutant plants with a variable extent of leaf rolling and some phenotypically normal plants from self-progenies of #22448. Plant #22448 was selfed and crossed with several mutant parents and F_1 plants to obtain additional genetic data. Table 1 presents origins and general

Table 1. Origin and general description of plant materials.

Serial Plant Number	Number of Plants	Origin	Description
22448	1	1624 x 9723	Original segregant for rolled-leaf mutant plants
22603, 22707, 22709, 24573 - 24718, 26070 - 26157, 26960 - 27069	365	22448 ⊗ " " " "	S_1 populations of #22448 from which mutant and normal plants were selected to be used in crosses with unrelated normal plants to produce F_1 populations
9814	1	Wisc 2-7	Genetically unrelated normal plants used in crosses with mutant or normal S_1 plants of #22448 to produce F_1 populations
24135	1	"Polar"	
24251	1	"Manchar"	
24800 - 24810	11	24668 x 9814	F_1
24811	1	24589 x 24251	"
24812 - 24814	3	24646 x 24251	"
24815	1	24712 x 24251	"
24816 - 24824	9	22603 x 9814	"
24825	1	24659 x 9814	"
24826	1	24579 x 24251	"
24827, 24828	2	24654 x 9814	"
24829	1	24653 x 9814	"
24830 - 24832	3	24638 x 9814	"
24833 - 24847	15	24673 x 24251	"
24848 - 24853	6	9814 x 24670	"
24854	1	24627 x 9814	"
24855, 24856	2	24599 x 24135	"
24857 - 24860	4	24650 x 9814	"
24861 - 24870	10	24577 x 24251	"
24871 - 24877	7	24251 x 24578	"
24878, 24879	2	24251 x 24583	"
24880 - 24881	2	24251 x 24660	"
24882 - 24884	3	22707 x 9814	"
25500 - 25672	173	24811 ⊗	F_2
25727 - 25807	71	24835 x 24837	"
26015 - 26044	30	24880 x 24660	BC_1
26258 - 26359	102	24866 ⊗	F_2
26480 - 26579	100	24846 x 24833	"
26749 - 26869	121	24876 x 24873	"
27121 - 27150	30	24583 x 24878	BC_1

descriptions of plant material used in this study.

Description of Mutant

A typical rolled-leaf mutant is shown in comparison with a normal plant in Fig. 1. The character is manifested in the very early stage of seedling growth, when the second leaf begins to emerge. Narrow and rather thick leaf blades fold inward from the leaf margins toward the midvein to a varying extent. Figures 2, 3, and 4 illustrate the wide range of continuous variation among mutant progenies from a certain F_2 family. A uniform expression of leaf rolling was exhibited among mutant progenies from some segregating families. In extreme cases, the leaf blades fail to unfold and release the subsequent leaf blades, resulting in the formation of "loops". Loops may be single or multiple depending on the number of leaves involved in the loop formation. However, in some instances, the leaves do not form loops, although the leaf rolling is very extreme. The formation of loops is purely mechanical. The loop may open if the subsequent leaves are forced to be released. In intermediate cases, some mutants exhibit leaf rolling only in the middle of the first leaf blade so that the leaf blade gradually opens to normal near the tip and base of the leaf blade. The new leaves develop

normally thereafter. This recovered normal plant can not be distinguished from originally normal individuals. In these individuals, mutant characteristics may be manifested again on newly emerging tillers or new growth after clipping. The classification is good for the extreme plants and fair for the intermediate. It was observed that the expression of mutant characteristics in the seedling stage was unaffected by temperature or photoperiod.

Mutants are less vigorous than normal plants. Mutants with extreme rolled-leaf are so weak that many winter-kill easily, and some die even in the greenhouse. Most mutant plants matured later than normal plants. They have a smaller number of heads and spikelets than normal plants. Mutants are mostly self- or male-sterile. Male-sterile plants have abnormal, small anthers which usually dry up near anthesis. A small amount of viable pollen grains was observed under the microscope from some mutant plants. The mechanism of this poor development of the anthers is not known.

Plant Culture and Crossing

Experiments were conducted in the field at the Agronomy Research Farm of the University of New Hampshire, Madbury, New Hampshire, U.S.A., and in the research

greenhouses of the Department of Plant Science. Plants were treated for maximum tillering and flowering in the greenhouse (28). Seedlings selected from self progenies of #22448 were grown in a cool house at 16 C with a 10-hour photoperiod for four months. They were transferred to a warm house at 27 C with a 16-hour photoperiod. In about six weeks in a warm house, florets were scissor-emasculated (S.E.) about 2 days before anthesis and pollinated by the selected normal male parents to produce F_1 seeds under bags or in isolation. Reciprocals were also made. Seeds were harvested 6 weeks after pollination. The F_1 seeds were planted immediately after harvest in August 1975 and grown in a cool house for four months. The F_2 plants were obtained by selfing of F_1 plants or by mutual pollination (M.P.) between F_1 sibs during February, 1976. Mutual pollination was practiced to alleviate a drastic inbreeding depression upon selfing. Only a few mutants were planted because they were too weak to set enough seeds to use in analysis. Mostly normal F_2 plants were transplanted to a spaced nursery (1.07 x 1.07 m) during May, 1976. Some F_1 plants also were transplanted to the field in late April, 1976 to obtain additional F_2 seeds for genetic analysis. These F_1 and F_2 plants transplanted in April produced heads during July, 1976, about one month later

than normal heading time in New Hampshire. Although only a small amount of seed was obtained from late-headed plants, it was enough to determine self-fertile families. Twelve segregating F_2 families were planted in April, 1976 with an average of 120 plants per family. In July, 1976 the 5 most self-fertile families could be selected for further selfing by bagging all 12 families. These 5 F_2 families were selfed to obtain F_3 seeds in June, 1977. Backcross progenies were obtained by crossing F_1 plants to mutant parents with a scissor emasculation (S.E.) method. Clones were brought into the greenhouse in the first week of November, 1975 and 1976, to obtain additional backcross seeds. They were cultured to promote maximum tillering and flowering in the greenhouse and were crossed during February and March, 1976 and 1977. Ten segregating BC_1 families were planted in April, 1976 with an average of 60 plants per family. In July, 1976 the 4 most self-fertile families could be selected for further selfing by bagging all 10 families. These 4 familes were selfed in June, 1977. Crosses were made between #22448 and several mutant parents and other F_1 plants to obtain additional genetic data. Reciprocals were also made where possible.

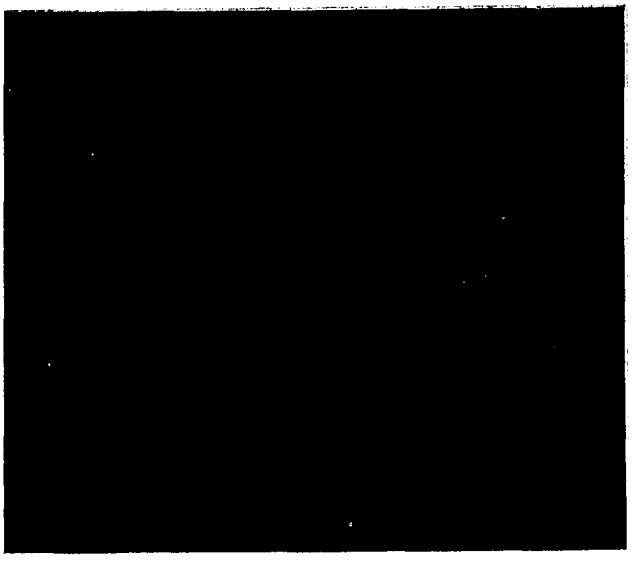
Scoring and Statistical Analysis

Seeds were planted in Jiffy-Mix and grown in the greenhouse usually at 20 to 30 C with 13 to 16-hour photoperiod until they were ready to be scored. When light and heavy seeds were planted separately, no relationships were found between segregation ratios and the weight of seed or germination rates. Seedlings were scored visually 4 - 5 weeks after germination when they were usually in the 3 - 4 leaf stage. Considering the variable expression of this mutant character, plants were rated in some families in an attempt to determine gene dosage effect. The rating of seedlings was made as follows. 1) Rolled-A (r-A); for the extreme rolled, leaves were so tightly rolled that they often showed a needle-like appearance, and usually formed double or multiple loops (Fig. 2 and 3). 2) Rolled-B (r-B); for those between r-A and r-C. 3) Rolled-C (r-C); for the intermediates. 4) Rolled-D (r-D); for the least rolled. A rolled-D plant could have the first leaf rolled and the second be normal. For most families, all mutants with various expressions of leaf-rolling were combined. A X^2-test was employed for goodness-of-fit for the genotypic ratios in S_1 plants from #22448 and BC_1, and F_2 families. No statistical test was possible for a phenotypic

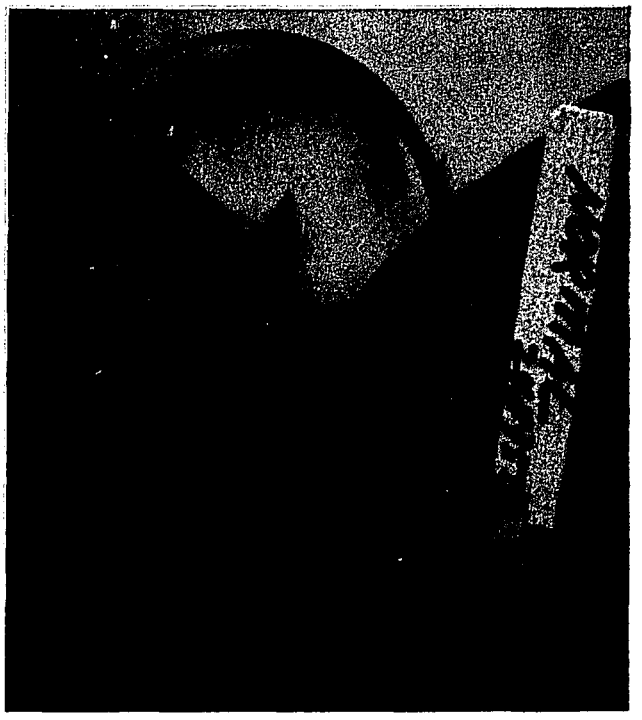
ratio in each self or cross because of the variable expected value to be discussed later.

Cytology

Cytological observations were made on root-tips of the parents and some of the F_1 plants. Somatic chromosome counts were made according to a technique used in a laboratory of Dr. Ralph Riley of Cambridge, U.K. for somatic chromosomes of cereals. Root-tips were collected from the pots around 3 PM, and pretreated in a freshly prepared saturated solution of 1-bromo-naphthalene in tap water for 4 hours. The naphthalene was replaced with glacial acetic acid for 24 hours. Then, the root-tips were hydrolyzed with 1N HCl at 60 C for about 12 minutes. The HCl was replaced with leucobasic fuchsin for 20 to 30 min to stain the roots. The stained root-tips were cut off and placed in a drop of 45% acetic acid on a glass slide to be squashed.



A



B

Fig. 1. A; Typical rolled-leaf mutant, and
B; Normal plant of Bromus inermis at 10 weeks after germination.

Fig. 2. Variation in leaf rolling character among rolled-leaf mutants of Bromus inermis. Rolled-A (right) is the extreme form.

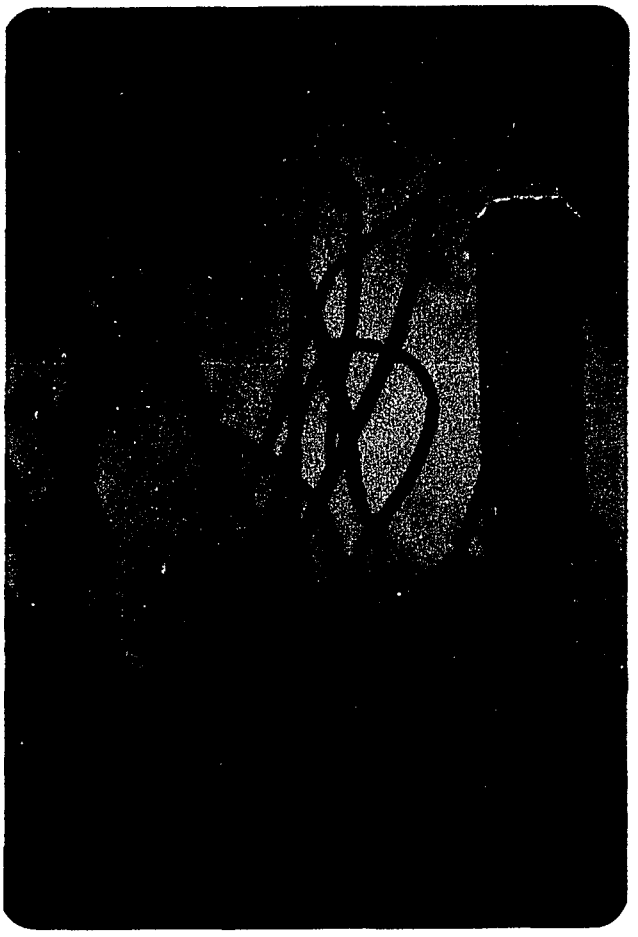


Fig. 3. Close-up of the extreme rolled-leaf mutant of *Bromus inermis*.

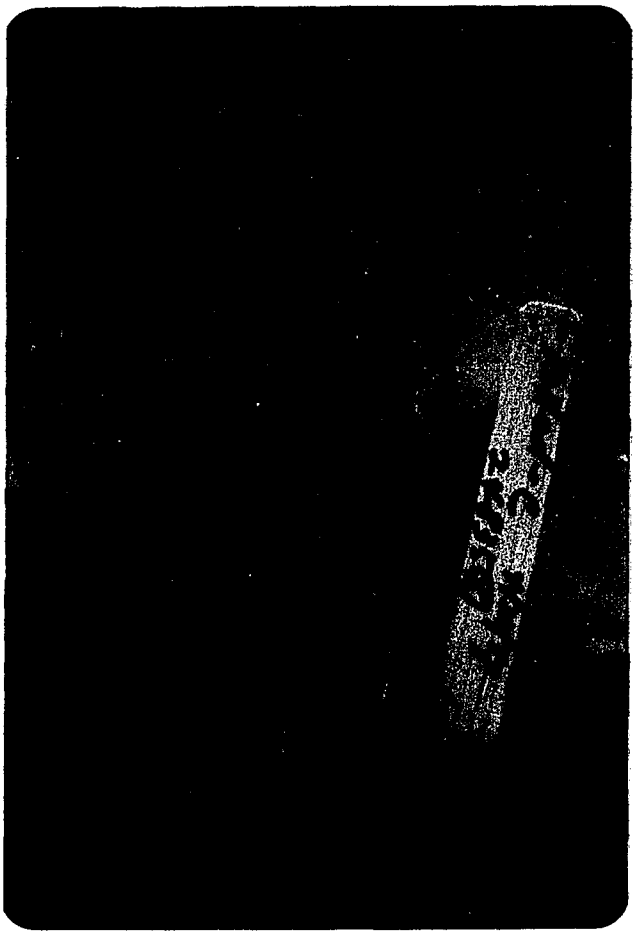


Fig. 4. Close-up of the intermediate rolled-leaf mutant of Bromus inermis.

RESULTS

Segregation in Parental Populations

The segregation data from selfing plant No. 22448 (#22448), and normal and mutant parents are shown in table 2. Also presented in table 2 are expected phenotypic ratios of normal to mutant (R/r ratio) and a proposed genotype for each plant. Expected ratios were calculated according to the proposed mode of inheritance derived from this study. The incompletely dominant normal allele of the rolled-leaf gene was represented by the symbol "R", and the recessive mutant allele by the symbol "r". Derivation of the expected R/r ratio and a method for assignment of proposed genotypes will be presented in the following section. Since the segregation ratios within a plant varied between years, the data when available were presented separately for both years. Plant #22448 segregated in an R/r ratio of 4.6 : 1 in both years. Cytological evidence for genomic constitutions in the literature and observed genetic data led to an assumption of simple tetrasomic inheritance. The excess of recessives in the S_1 population of #22448 could not be explained without further assumptions. Plant #22448 was an

Table 2. Segregations of #22448, and of normal and mutant parents for the rolled-leaf character.

Plant	Origin	Observed 1976 R	1976 r	1976 R/r	Observed 1977 R	1977 r	1977 R/r	Expected[a] R/r Ratio	Proposed Genotype
22448-R[b]	1624 S.E. x 9723	911	198	4.6	2927	636	4.6	2.4	RRrr
9814 -R	Wisc 2-7	927	0	-	1372	0	-	-	RRRR
24135-R	"Polar"	1213	0	-	1308	0	-	-	RRRR
24251-R	"Manchar"	1101	0	-	1445	0	-	-	RRRR
22707-A	22448 ⊗	-	-	-	10	17	0.6	0.3	Rrrr
22709-A	"	-	-	-	50	202	0.3	0.3	Rrrr
24578-A	"	-	-	-	13	35	0.4	0.3	Rrrr
24602-B	"	-	-	-	0	16	-	-	rrrr
24660-D	"	-	-	-	27	66	0.4	0.3	Rrrr
24670-R	"	-	-	-	1075	146	7.4	2.4	RRrr
24671-R	"	-	-	-	1057	20	52.9	26.4	RRRr
24672-R	"	-	-	-	47	6	7.8	2.4	RRrr
24673-R	"	-	-	-	2677	17	157.5	26.4	RRRr

[a] Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b] Seedling phenotypes rated for the extent of leaf rolling character in each plant. A for the extreme, B for those between A and C, C for the intermediate, D for the least rolled plants, and R for the normal plants.

F_1 between phenotypically normal #1624 and #9723. If it were in a disomic one, two, or three factor condition, it should have segregated in an R/r ratio of 3.0, 15.0, or 63.0 : 1 respectively upon selfing. If it were in a hexasomic or octosomic condition, it should have segregated in an R/r ratio of 399.0 or 4899.0 : 1, respectively, upon selfing. Neither complete dominance in hexasomic or octosomic condition, nor complementary gene action in the disomic condition could account for the surplus recessives in the segregation of #22448. When an observed ratio of 4.6 : 1 was obtained from over 4600 progenies, there must have been a genetic basis for this segregation other than chance error.

Three self-fertile normal plants, used as parents in crosses did not segregate for the rolled-leaf character during the two year period. It was assumed that these normal parents, #9814, #24135, and #24251 were homozygous for dominant alleles, RRRR. Most of the mutants were weak and largely self-incompatible or male-sterile. Only five of 144 rolled plants produced a few selfed seeds. Plant #24602 did not segregate any normal phenotypes and was assumed to be homozygous recessive, rrrr. The plant was intermediate for the rolled trait indicating that there was no direct

relationship between the extent of leaf rolling and the dose of recessive alleles. The other three mutant plants segregated in the R/r ratios of 0.3, 0.4 and 0.6 : 1 although they were extremely rolled. Therefore, incomplete dominance was assumed. Four phenotypically normal plants, #24670 to #24673, segregated in an R/r ratio of 7.4, 52.9, 7.8, and 157.5 : 1, respectively.

More S_1 plants from #22448 were planted in the summer of 1976. The S_2 segregation data obtained from 86 plants are presented in table 3. Only four plants did not segregate for the rolled-leaf character. All others segregated in the R/r ratios ranging from 0.2 : 1 to 269.0 : 1.

Segregation in F_2

Table 4 presents F_2 segregation ratios for the rolled-leaf character over a two-year period. The data could not be combined because of significant differences between years on the same plant. For example, #24811 segregated in an R/r ratio of 33.1 : 1 in 1976 but 333.0 : 1 in 1977. Plant #24842 segregated in an R/r ratio of 1274.0 : 1 in 1976 and 126.5 : 1 in 1977. Plant #24849 segregated in an R/r ratio of 179.8 : 1 in 1976, and 1115.0 : 1 in 1977. Overall, 3 to 5 fold differences were commonly observed.

Table 3. S_2 segregation from #22448 for the rolled-leaf character.

S_1	Phenotype	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26078[b]	rolled	4	4	1.0	0.3	Rrrr
26086	"	1	6	0.2	0.3	Rrrr
26092	"	11	4	2.8	0.3	Rrrr
26094	"	5	2	2.5	0.3	Rrrr
26111	"	1	2	0.5	0.3	Rrrr
26116	"	1	3	0.3	0.3	Rrrr
26960	normal	228	35	6.5	2.4	RRrr
26961	"	201	13	15.5	2.4	RRrr
26962	"	770	8	96.3	26.4	RRRr
26965	"	1054	116	9.1	2.4	RRrr
26966	"	256	0	-	-	RRRR
26968	"	734	12	61.2	26.4	RRRr
26970	"	136	34	4.0	2.4	RRrr
26971	"	166	3	55.3	26.4	RRRr
26973	"	404	44	9.2	2.4	RRrr
26974	"	70	7	10.0	2.4	RRrr
26975	"	299	4	74.8	26.4	RRRr
26976	"	114	14	8.1	2.4	RRrr
26978	"	13	1	13.0	2.4	RRrr
26979	"	281	0	-	-	RRRR
26980	"	213	6	35.5	26.4	RRRr
26981	"	661	144	4.6	2.4	RRrr
26982	"	807	3	269.0	26.4	RRRr
26983	"	415	17	24.4	2.4	RRrr
26984	"	151	1	151.0	26.4	RRRr
26986	"	18	6	3.0	2.4	RRrr
26988	"	114	38	3.0	2.4	RRrr

Table 3. Continued.

S_1	Phenotype	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26990	normal	268	24	11.2	2.4	RRrr
26991	"	435	70	6.2	2.4	RRrr
26992	"	46	8	5.8	2.4	RRrr
26993	"	333	37	9.0	2.4	RRrr
26994	"	419	33	12.7	2.4	RRrr
26995	"	429	4	107.3	26.4	RRRr
26997	"	376	61	6.2	2.4	RRrr
26998	"	35	6	5.8	2.4	RRrr
27000	"	274	3	91.3	26.4	RRRr
27002	"	352	25	14.1	2.4	RRrr
27003	"	600	82	7.3	2.4	RRrr
27004	"	584	16	36.5	26.4	RRRr
27005	"	79	8	9.9	2.4	RRrr
27006	"	282	27	10.4	2.4	RRrr
27007	"	52	12	4.3	2.4	RRrr
27008	"	447	79	5.7	2.4	RRrr
27009	"	23	1	23.0	2.4	RRrr
27010	"	156	24	6.5	2.4	RRrr
27013	"	45	2	22.5	2.4	RRrr
27014	"	448	13	34.5	26.4	RRRr
27015	"	252	7	36.0	26.4	RRRr
27016	"	540	21	25.7	2.4	RRrr
27017	"	91	3	30.3	26.4	RRRr
27021	"	755	23	32.8	26.4	RRRr
27022	"	180	3	60.0	26.4	RRRr
27023	"	520	109	4.8	2.4	RRrr
27024	"	406	24	16.9	2.4	RRrr

Table 3. Continued.

S_1	Phenotype	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
27025	normal	400	56	7.1	2.4	RRrr
27027	"	519	62	8.4	2.4	RRrr
27028	"	197	6	32.8	26.4	RRRr
27029	"	225	10	22.5	2.4	RRrr
27030	"	679	93	7.9	2.4	RRrr
27032	"	102	13	7.9	2.4	RRrr
27033	"	337	41	8.2	2.4	RRrr
27034	"	554	82	6.8	2.4	RRrr
27036	"	644	19	33.9	26.4	RRRr
27038	"	381	72	5.3	2.4	RRrr
27039	"	207	35	5.9	2.4	RRrr
27040	"	144	2	72.0	26.4	RRRr
27041	"	155	2	77.5	26.4	RRRr
27042	"	46	3	15.3	2.4	RRrr
27043	"	1269	13	97.6	26.4	RRRr
27045	"	216	3	72.0	26.4	RRRr
27046	"	692	37	18.7	2.4	RRrr
27047	"	270	18	15.0	2.4	RRrr
27048	"	28	2	14.0	2.4	RRrr
27049	"	149	22	6.8	2.4	RRrr
27050	"	103	16	6.4	2.4	RRrr
27051	"	112	9	12.4	2.4	RRrr
27056	"	118	0	-	-	RRRR
27058	"	328	5	65.6	26.4	RRRr
27060	"	143	30	4.8	2.4	RRrr
27061	"	490	97	5.1	2.4	RRrr
27063	"	289	5	57.8	26.4	RRRr

Table 3. Continued.

S_1	Phenotype	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
27064	normal	7	2	3.5	2.4	RRrr
27065	"	133	0	-	-	RRRR
27067	"	475	62	7.7	2.4	RRrr
27068	"	248	22	11.3	2.4	RRrr
27069	"	262	2	131.0	26.4	RRRr

[a]Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b]Plants underlined were rolled as a seedling.

Table 4. Segregation in F_2 for the rolled-leaf character.

F_1	Origin	Observed 1976 R	1976 r	1976 R/r	Observed 1977 R	1977 r	1977 R/r	Expected[a] R/r Ratio	Proposed Genotype
Section 1									
24802	24668 S.E. x 9814	98	2	49.0	179	3	59.7	26.4	RRRr
24803	"	123	2	61.5	98	0	-	26.4	RRRr
24804	"	600	11	54.6	426	6	71.0	26.4	RRRr
24805	"	134	5	26.8	204	2	102.0	26.4	RRRr
24806	"	109	1	109.0	45	0	-	26.4	RRRr
24807	"	7	1	7.0	12	2	6.0	2.4	RRrr
24809	"	-	-	-	143	3	47.7	26.4	RRRr
24810	"	10	0	-	136	3	45.3	26.4	RRRr
24811	24589 S.E. x 24251	331	10	33.1	666	2	333.0	26.4	RRRr
24812	24646 S.E. x 24251	563	3	187.7	949	4	237.3	26.4	RRRr
24813	"	104	0	-	188	1	188.0	26.4	RRRr
24814	"	791	3	263.7	1121	3	373.7	26.4	RRRr
24815	24712 S.E. x 24251	163	2	81.5	143	0	-	26.4	RRRr
24816	22603 S.E. x 9814	196	3	65.3	269	2	134.5	26.4	RRRr
24818	"	115	0	-	158	2	79.0	26.4	RRRr
24817	"	20	1	20.0	412	24	17.2	2.4	RRrr
24820	"	29	0	-	395	9	43.9	26.4	RRRr
24821	"	-	-	-	360	3	120.0	26.4	RRRr
24822	"	552	0	-	1115	5	223.0	26.4	RRRr
24823	"	5	0	-	18	1	18.0	2.4	RRrr
24824	"	9	1	9.0	127	18	7.1	2.4	RRrr
24825	24659 S.E. x 9814	241	5	48.2	888	29	30.6	26.4	RRRr
24826	24579 S.E. x 24251	300	7	42.9	333	0	-	26.4	RRRr
24828	24654 S.E. x 9814	-	-	-	245	3	81.6	26.4	RRRr
24829	24653 S.E. x 9814	38	3	12.7	73	4	18.3	2.4	RRrr

Table 4. Continued.

F1	Origin	Observed 1976 R	1976 r	1976 R/r	Observed 1977 R	1977 r	1977 R/r	Expected[a] R/r Ratio	Proposed Genotype
Section 1 (Continued)									
24830	24638 S.E. x 9814	583	11	53.0	1265	30	42.2	26.4	RRRr
24831	"	-	-	-	925	12	77.1	26.4	RRRr
24832	"	112	2	56.0	216	3	72.0	26.4	RRRr
24854	24627 S.E. x 9814	109	2	54.5	539	18	29.9	26.4	RRRr
24856	24599 S.E. x 24135	36	4	9.0	-	-	-	2.4	RRrr
24857	24650 S.E. x 9814	-	-	-	32	5	6.4	2.4	RRrr
24858	"	93	3	31.0	153	0	-	26.4	RRRr
24860	"	31	0	-	131	2	65.5	26.4	RRRr
24862	24577 S.E. x 24251	194	1	194.0	42	0	-	26.4	RRRr
24863	"	102	1	102.0	978	4	244.5	26.4	RRRr
24864	"	-	-	-	139	2	69.5	26.4	RRRr
24866	"	241	1	241.0	851	1	851.0	26.4	RRRr
24868	"	26	0	-	791	4	197.8	26.4	RRRr
24869	"	1783	6	297.2	1543	46	33.5	26.4	RRRr
24870	"	415	8	51.9	161	3	53.7	26.4	RRRr
Section 2									
24871	24251 S.E. x 24578	-	-	-	172	1	172.0	26.4	RRRr
24872	"	-	-	-	82	7	11.9	2.4	RRrr
24873	"	100	1	100.0	693	3	231.0	26.4	RRRr
24874	"	1101	22	50.1	791	5	158.2	26.4	RRRr
24875	"	12	1	12.0	575	8	71.9	26.4	RRRr

Table 4. Continued.

F_1	Origin	Observed 1976 R	1976 r	1976 R/r	Observed 1977 R	1977 r	1977 R/r	Expected[a] R/r Ratio	Proposed Genotype
Section 2 (Continued)									
24876	24251 S.E. x 24578	544	8	68.0	329	9	36.6	26.4	RRRr
24877	"	1274	17	74.9	1597	19	84.1	26.4	RRRr
24878	24251 S.E. x 24583	21	0	-	1108	6	84.7	26.4	RRRr
24879	"	449	9	49.9	481	7	68.7	26.4	RRRr
24880	24251 S.E. x 24660	1423	3	474.3	377	0	-	26.4	RRRr
24881	"	343	3	114.3	1169	8	146.1	26.4	RRRr
Section 3									
24833	24673 S.E. x 24251	135	0	-	129	2	64.5	26.4	RRRr
24835	"	453	21	21.6	778	30	26.3	2.4	RRrr
24836	"	709	0	-	113	0	-	-	RRRR
24837	"	837	3	279.0	741	0	-	26.4	RRRr
24838	"	492	0	-	1434	0	-	-	RRRR
24839	"	297	0	-	210	0	-	-	RRRR
24840	"	777	0	-	1267	8	158.4	26.4	RRRr
24841	"	62	0	-	30	0	-	-	?
24842	"	1274	1	1274.0	1391	11	126.5	26.4	RRRr
24843	"	80	1	80.0	41	1	41.0	26.4	RRRr
24844	"	1489	0	-	94	1	94.0	26.4	RRRr
24845	"	122	0	-	1359	0	-	-	RRRR
24846	"	852	14	60.9	1221	2	610.5	26.4	RRRr

Table 4. Continued.

F_1	Origin	Observed 1976 R	1976 r	1976 R/r	Observed 1977 R	1977 r	1977 R/r	Expected[a] R/r Ratio	Proposed Genotype
Section 4									
24849	9814 S.E. x 24670	889	5	179.8	1115	1	1115.0	26.4	RRRr
24850	"	7	1	7.0	303	5	60.6	26.4	RRRr
24851	"	13	2	6.5	164	2	82.0	26.4	RRRr
24852	"	5	0	-	63	0	-	-	?
24853	"	729	8	91.1	813	5	162.6	26.4	RRRr

[a] Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

Thus, a wide range of segregation ratios occurs within a plant under different environmental conditions as well as between plants. This further complicates the classification or identification of genotypes within a family. The fixed ratio for a certain genotype may not be applicable for this type of inheritance pattern.

Forty F_1 plants, listed in the first section of table 4, were produced from crosses between several different mutant plants and unrelated normal parents. Eleven F_1 plants, listed in section 2, were obtained by reciprocal crosses in which mutant plants were used as pollen parents. Sections 3 and 4 include F_1 plants derived from genotypically normal carriers of the rolled-leaf character. There were not enough F_1 plants from a single cross to indicate an inheritance pattern. However, the data in the first section of table 4 may be combined among F_1 plants from the crosses of mutant x normal. All F_1 plants were phenotypically normal and vigorous in growth, indicating that the rolled-leaf character is recessive to the normal phenotype. The F_2 segregation ratios ranged from 6.0 to 851.0 : 1. An attempt was made to detect some tendencies for segregation ratios to cluster about certain ratios. This proved impossible because of the variation of the ratios between years within a plant. The variation in segregation ratios

within a plant may not be solely the influence of environment because there were not consistent yearly differences among the plants. Interaction between the genotype and environment might have occurred. Thus, the F_2 segregation indicated again the heterozygosity of mutant parents. The wide range of variation in segregation ratios was totally unexpected if the mutant were homozygous recessive. Incomplete dominance of the gene action was therefore assumed.

Segregation in F_3

Tables 5 through 9 present the segregation in F_3 populations for the rolled-leaf character. Because mostly normal F_2 plants were planted, the classification and test of genotypic ratios within a family were limited to phenotypically normal plants, or to assumed quadruplex (RRRR), triplex (RRRr), and duplex (RRrr) individuals.

Segregation in BC_1

Table 10 presents, a) the segregation ratios in backcross populations, b) the estimated average percent transmission of homozygous recessive gametes (AT-rr rate) in pollen and seed parents, and c) proposed genotypes. An incomplete transmission of homozygous recessive gametes was indicated by the deficiency of duplex individuals in F_1

Table 5. F_3 segregation from F_2 progenies from #24811.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
25505[b]	24811 ⊗	60	1	60.0	26.4	RRRr
25506	"	776	3	258.7	26.4	RRRr
25508	"	470	0	-	-	RRRR
25519	"	186	0	-	-	RRRR
25520	"	59	2	29.5	26.4	RRRr
25522	"	122	4	30.5	26.4	RRRr
25523	"	61	0	-	-	RRRR
25528	"	87	2	43.5	26.4	RRRr
25529	"	64	0	-	-	RRRR
25535	"	8	2	4.0	2.4	RRrr
25545	"	1	1	1.0	0.3	Rrrr
25547	"	109	34	3.2	2.4	RRrr
25557	"	352	1	352.0	26.4	RRRr
25558	"	203	3	67.7	26.4	RRRr
25559	"	111	0	-	-	RRRR
25562	"	94	17	5.5	2.4	RRrr
25571	"	1	1	1.0	0.3	Rrrr
25572	"	153	1	153.0	26.4	RRRr
25573	"	33	11	3.0	2.4	RRrr
25575	"	34	5	6.8	2.4	RRrr
25579	"	81	0	-	-	RRRR
25582	"	152	2	76.0	26.4	RRRr
25588	"	4	1	4.0	2.4	RRrr
25589	"	139	2	69.5	26.4	RRRr
25591	"	179	2	89.5	26.4	RRRr
25592	"	2690	0	-	-	RRRR
25595	"	228	1	228.0	26.4	RRRr

Table 5. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
25629	24811 ⊗	49	1	49.0	26.4	RRRr
25632	"	164	20	8.2	2.4	RRrr
25634	"	46	4	11.5	2.4	RRrr
25637	"	85	2	42.5	26.4	RRRr
25647	"	43	1	43.0	26.4	RRRr
25648	"	122	0	-	-	RRRR
25655	"	154	2	77.1	26.4	RRRr
25662	"	121	0	-	-	RRRR
25663	"	50	1	50.0	26.4	RRRr
25665	"	79	0	-	-	RRRR

[a] Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b] Plants underlined were rolled as a seedling.

Table 6. F_3 segregation from F_2 progenies from #24866.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26259	24866 ⊗	556	8	69.5	26.4	RRRr
26260	"	67	2	33.5	26.4	RRRr
26261	"	218	1	218.0	26.4	RRRr
26262	"	45	1	45.0	26.4	RRRr
26263	"	211	0	-	-	RRRR
26264	"	437	0	-	-	RRRR
26265	"	179	0	-	-	RRRR
26266	"	155	0	-	-	RRRR
26267	"	154	0	-	-	RRRR
26274	"	136	1	136.0	26.4	RRRr
26275	"	257	0	-	-	RRRR
26277	"	273	3	91.0	26.4	RRRr
26278	"	149	0	-	-	RRRR
26279	"	122	0	-	-	RRRR
26280	"	161	0	-	-	RRRR
26284	"	31	2	15.5	2.4	RRrr
26285	"	182	0	-	-	RRRR
26287	"	452	9	50.2	26.4	RRRr
26288	"	138	8	17.3	2.4	RRrr
26289	"	304	1	304.0	26.4	RRRr
26290	"	131	0	-	-	RRRR
26291	"	86	6	14.3	2.4	RRrr
26292	"	919	0	-	-	RRRR
26293	"	365	0	-	-	RRRR
26294	"	550	0	-	-	RRRR
26295	"	428	2	214.0	26.4	RRRr
26296	"	118	3	39.3	26.4	RRRr
26297	"	45	5	9.0	2.4	RRrr

Table 6. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26298	24866 ⊗	110	8	13.8	2.4	RRrr
26299	"	226	0	-	-	RRRR
26303	"	139	2	69.5	26.4	RRRr
26304	"	142	3	47.3	26.4	RRRr
26305	"	287	3	95.7	26.4	RRRr
26306	"	122	2	61.0	26.4	RRRr
26307	"	62	1	62.0	26.4	RRRr
26308	"	44	1	44.0	26.4	RRRr
26309	"	492	0	-	-	RRRR
26310	"	137	2	68.5	26.4	RRRr
26311	"	341	3	113.7	26.4	RRRr
26312	"	482	6	80.3	26.4	RRRr
26313	"	117	2	58.5	26.4	RRRr
26314	"	327	19	17.2	2.4	RRrr
26315	"	83	1	83.0	26.4	RRRr
26316	"	155	1	155.0	26.4	RRRr
26318	"	54	3	18.0	2.4	RRrr
26319	"	104	2	52.0	26.4	RRRr
26320	"	782	2	393.5	26.4	RRRr
26322	"	117	2	58.5	26.4	RRRr
26323	"	162	1	162.0	26.4	RRRr
26324	"	827	22	37.6	26.4	RRRr
26325	"	420	6	70.0	26.4	RRRr
26327	"	626	0	-	-	RRRR
26328	"	294	2	147.0	26.4	RRRr
26329	"	151	3	50.3	26.4	RRRr
26330	"	327	5	65.4	26.4	RRRr
26331	"	495	26	19.0	2.4	RRrr

Table 6. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26332[b]	24866 ⊗	125	3	41.7	26.4	RRRr
26333	"	44	1	44.0	26.4	RRRr
26334	"	222	2	111.0	26.4	RRRr
26335	"	46	3	15.3	2.4	RRrr
26336	"	60	10	6.0	2.4	RRrr
26337	"	146	1	146.0	26.4	RRRr
26338	"	283	0	-	-	RRRR
26339	"	707	4	176.8	26.4	RRRr
26343	"	45	3	15.0	2.4	RRrr
26346	"	173	2	86.5	26.4	RRRr
26347	"	427	0	-	-	RRRR
26348	"	60	3	20.0	2.4	RRrr
26349	"	137	1	137.0	26.4	RRRr
26350	"	430	0	-	-	RRRR
26351	"	825	4	206.3	26.4	RRRr
26353	"	63	6	10.5	2.4	RRrr
26354	"	186	1	186.0	26.4	RRRr
26355	"	290	20	14.5	2.4	RRrr
26356	"	28	13	2.2	0.3	Rrrr
26357	"	120	2	60.0	26.4	RRRr
26358	"	549	0	-	-	RRRR
26359	"	22	1	22.0	26.4	RRRr

[a]Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b]Plants underlined were rolled as a seedling.

Table 7. F_3 segregation from a cross between the full-sibs, #24835 and #24837.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
25729[b]	24835 x 24837	696	12	58.0	26.4	RRRr
25730	"	71	1	71.0	26.4	RRRr
25732	"	494	2	247.0	26.4	RRRr
25733	"	585	0	-	-	RRRR
25734	"	478	2	239.0	26.4	RRRr
25736	"	246	1	246.0	26.4	RRRr
25737	"	146	5	29.2	26.4	RRRr
25738	"	130	1	130.0	26.4	RRRr
25739	"	269	2	134.5	26.4	RRRr
25740	"	675	7	96.4	26.4	RRRr
25741	"	443	34	13.0	2.4	RRrr
25742	"	393	0	-	-	RRRR
25743	"	354	0	-	-	RRRR
25745	"	60	4	15.0	2.4	RRrr
25746	"	67	1	67.0	26.4	RRRr
25747	"	142	11	12.9	2.4	RRrr
25748	"	343	3	114.3	26.4	RRRr
25749	"	696	12	58.0	26.4	RRRr
25750	"	49	2	24.5	2.4	RRrr
25751	"	101	6	16.8	2.4	RRrr
25752	"	73	1	73.0	26.4	RRRr
25753	"	272	92	3.0	2.4	RRrr
25754	"	838	6	139.7	26.4	RRRr
25755	"	166	17	9.8	2.4	RRrr
25756	"	11	10	1.1	0.3	Rrrr
25757	"	382	2	191.0	26.4	RRRr
25759	"	193	15	12.9	2.4	RRrr
25760	"	816	7	116.6	26.4	RRRr

Table 7. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
25761	24835 x 24837	395	11	35.9	26.4	RRRr
25762	"	1131	2	565.5	26.4	RRRr
25763	"	386	2	193.0	26.4	RRRr
25764	"	1663	4	415.8	26.4	RRRr
25766	"	122	3	40.7	26.4	RRRr
25767	"	933	0	-	-	RRRR
25768	"	705	5	141.0	26.4	RRRr
25769	"	116	4	29.0	26.4	RRRr
25770	"	42	2	21.0	2.4	RRrr
25771	"	80	4	20.0	2.4	RRrr
25773	"	1223	2	611.5	26.4	RRRr
25774	"	632	4	158.0	26.4	RRRr
25775	"	946	7	135.1	26.4	RRRr
25777	"	675	0	-	-	RRRR
25778	"	363	0	-	-	RRRR
25779	"	106	2	53.0	26.4	RRRr
25780	"	1176	117	10.1	2.4	RRrr
25781	"	682	151	4.5	2.4	RRrr
25783	"	1157	4	289.3	26.4	RRRr
25784	"	22	2	11.0	2.4	RRrr
25785	"	63	10	6.3	2.4	RRrr
25786	"	76	20	3.8	2.4	RRrr
25787	"	902	5	180.4	26.4	RRRr
25789	"	272	23	11.8	2.4	RRrr
25790	"	360	1	360.0	26.4	RRRr
25791	"	409	3	136.3	26.4	RRRr
25792	"	1182	0	-	-	RRRR
25793	"	931	49	19.0	2.4	RRrr

Table 7. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
25794	24835 x 24837	841	21	40.1	26.4	RRRr
25795	"	45	2	22.5	2.4	RRrr
25796	"	676	5	135.2	26.4	RRRr
25797	"	434	2	217.0	26.4	RRRr
25798	"	117	3	39.0	26.4	RRRr
25799	"	75	1	75.0	26.4	RRRr
25800	"	258	55	4.7	2.4	RRrr
25802	"	708	0	-	-	RRRR
25803	"	768	0	-	-	RRRR
25804	"	559	143	3.9	2.4	RRrr
25806	"	82	5	16.4	2.4	RRrr
25807	"	438	0	-	-	RRRR

[a]Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b]Plants underlined were rolled as a seedling.

Table 8. F_3 segregation from a cross between the full-sibs, #24846 and #24833.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26481[b]	24846 x 24833	927	0	-	-	RRRR
26482	"	394	5	78.8	26.4	RRRr
26483	"	203	0	-	-	RRRR
26487	"	168	1	168.0	26.4	RRRr
26488	"	554	3	186.7	26.4	RRRr
26489	"	439	6	73.2	26.4	RRRr
26490	"	116	2	58.0	26.4	RRRr
26491	"	441	0	-	-	RRRR
26495	"	232	1	232.0	26.4	RRRr
26496	"	25	3	8.3	2.4	RRrr
26497	"	33	5	6.6	2.4	RRrr
26500	"	1	14	0.1	0.3	Rrrr
26506	"	9	5	1.8	0.3	Rrrr
26507	"	167	0	-	-	RRRR
26508	"	919	0	-	-	RRRR
26510	"	445	3	148.3	26.4	RRRr
26511	"	59	7	8.4	2.4	RRrr
26513	"	59	1	59.0	26.4	RRRr
26514	"	487	0	-	-	RRRR
26516	"	69	1	69.0	26.4	RRRr
26517	"	332	5	66.4	26.4	RRRr
26518	"	40	3	13.3	2.4	RRrr
26520	"	95	18	5.3	2.4	RRrr
26521	"	414	0	-	-	RRRR
26424	"	522	1	522.0	26.4	RRRr
26525	"	39	3	13.0	2.4	RRrr
26527	"	52	4	13.0	2.4	RRrr
26530	"	184	5	36.8	26.4	RRRr

Table 8. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26532	24846 x 24833	134	9	14.9	2.4	RRrr
26534	"	37	5	7.4	2.4	RRrr
26536	"	301	0	-	-	RRRR
26537	"	104	0	-	-	RRRR
26538	"	66	1	66.0	26.4	RRRr
26540	"	132	8	16.5	2.4	RRrr
26541	"	47	1	47.0	26.4	RRRr
26542	"	344	3	114.7	26.4	RRRr
26543	"	167	0	-	-	RRRR
26544	"	602	0	-	-	RRRR
26547	"	365	3	121.7	26.4	RRRr
26548	"	390	5	78.0	26.4	RRRr
26549	"	590	0	-	-	RRRR
26550	"	556	0	-	-	RRRR
26552	"	72	4	18.0	2.4	RRrr
26553	"	164	25	6.6	2.4	RRrr
26554	"	297	15	19.8	2.4	RRrr
26556	"	2208	7	315.4	26.4	RRRr
26557	"	63	2	31.5	26.4	RRRr
26558	"	290	13	22.3	2.4	RRrr
26560	"	75	2	37.5	26.4	RRRr
26561	"	147	2	73.5	26.4	RRRr
26562	"	400	2	200.0	26.4	RRRr
26564	"	97	12	8.1	2.4	RRrr
26565	"	329	0	-	-	RRRR
26567	"	182	11	16.5	2.4	RRrr
26569	"	184	0	-	-	RRRR
26570	"	341	1	341.0	26.4	RRRr
26572	"	76	1	76.0	26.4	RRRr

Table 8. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26575	24846 x 24833	1538	0	-	-	RRRR
26576	"	43	1	43.0	26.4	RRRr
26577	"	518	4	129.5	26.4	RRRr
26578	"	550	10	55.0	26.4	RRRr
26579	"	1047	0	-	-	RRRR

[a]Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b]Plants underlined were rolled as a seedling.

Table 9. F_3 segregation from a cross between the full-sibs, #24876 and #24873.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26750	24876 x 24873	90	2	45.0	26.4	RRRr
26752	"	129	0	-	-	RRRR
26754	"	289	0	-	-	RRRR
26755	"	944	3	314.7	26.4	RRRr
26756	"	1026	10	102.6	26.4	RRRr
26757	"	38	3	12.7	2.4	RRrr
26758	"	376	0	-	-	RRRR
26759	"	154	2	77.0	26.4	RRRr
26761	"	330	11	30.0	26.4	RRRr
26762	"	101	1	101.0	26.4	RRRr
26763	"	155	0	-	-	RRRR
26764	"	77	4	19.3	2.4	RRrr
26765	"	25	2	12.5	2.4	RRrr
26766	"	35	3	11.7	2.4	RRrr
26767	"	104	7	14.9	2.4	RRrr
26768	"	219	0	-	-	RRRR
26769	"	269	8	33.6	26.4	RRRr
26770	"	65	1	65.0	26.4	RRRr
26771	"	150	0	-	-	RRRR
26772	"	157	8	19.6	2.4	RRrr
26775	"	103	3	34.3	26.4	RRRr
26777	"	110	0	-	-	RRRR
26778	"	272	5	54.4	26.4	RRRr
26780	"	20	3	6.7	2.4	RRrr
26781	"	308	1	308.0	26.4	RRRr
26783	"	279	19	14.7	2.4	RRrr
26785	"	213	16	16.7	2.4	RRrr
26787	"	751	7	107.3	26.4	RRRr

Table 9. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26788[b]	24876 x 24873	423	4	105.8	26.4	RRRr
26789	"	542	10	54.2	26.4	RRRr
26790	"	23	4	5.8	2.4	RRrr
26792	"	196	0	-	-	RRRR
26795	"	277	0	-	-	RRRR
26798	"	178	0	-	-	RRRR
26800	"	113	9	12.6	2.4	RRrr
26802	"	113	3	37.7	26.4	RRRr
26804	"	46	1	46.0	26.4	RRRr
26806	"	133	1	133.0	26.4	RRRr
26807	"	610	5	122.0	26.4	RRRr
26808	"	434	0	-	-	RRRR
26809	"	208	1	208.0	26.4	RRRr
26811	"	105	0	-	-	RRRR
26812	"	432	3	144.0	26.4	RRRr
26813	"	211	0	-	-	RRRR
26815	"	118	0	-	-	RRRR
26816	"	310	3	103.3	26.4	RRRr
26817	"	238	6	39.7	26.4	RRRr
26819	"	79	1	79.0	26.4	RRRr
26820	"	284	8	35.5	26.4	RRRr
26826	"	395	3	131.7	26.4	RRRr
26827	"	46	9	5.1	2.4	RRrr
26828	"	2	7	0.3	0.3	Rrrr
26829	"	5	1	5.0	2.4	RRrr
26833	"	110	2	55.0	26.4	RRRr
26835	"	18	1	18.0	2.4	RRrr
26836	"	522	0	-	-	RRRR

Table 9. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26838	24876 x 24873	235	0	-	-	RRRR
26839	"	57	6	9.5	2.4	RRrr
26840	"	97	5	19.4	2.4	RRrr
26841	"	358	0	-	-	RRRR
26842	"	664	0	-	-	RRRR
26843	"	896	10	89.6	26.4	RRRr
26845	"	371	0	-	-	RRRR
26846	"	68	2	34.0	26.4	RRRr
26847	"	356	0	-	-	RRRR
26848	"	684	11	62.2	26.4	RRRr
26849	"	331	2	165.5	26.4	RRRr
26850	"	400	0	-	-	RRRR
26851	"	239	6	39.8	26.4	RRRr
26852	"	83	2	41.5	26.4	RRRr
26853	"	24	1	24.0	2.4	RRrr
26854	"	68	5	13.6	2.4	RRrr
26855	"	371	5	74.2	26.4	RRRr
26856	"	525	10	52.5	26.4	RRRr
26857	"	116	0	-	-	RRRR
26858	"	99	0	-	-	RRRR
26860	"	534	3	178.0	26.4	RRRr
26861	"	349	3	116.3	26.4	RRRr
26862	"	532	2	266.0	26.4	RRRr
26863	"	69	4	17.3	2.4	RRrr
26864	"	544	181	3.0	2.4	RRrr
26865	"	313	9	34.8	26.4	RRRr
26867	"	166	5	33.2	26.4	RRRr

Table 9. Continued.

F_2	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
24868	24876 x 24873	81	4	20.3	2.4	RRrr
26869	"	467	4	116.8	26.4	RRRr

[a] Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b] Plants underlined were rolled as a seedling.

Table 10. Segregation in backcross for rolled-leaf character.

Cross	Observed			% rr[a] Gamete	Genotype
	Normal(R)	Rolled(r)	R/r		
24579[b] S.E. x 24873	68	4	17.0	11.3	Rrrr x RRRr
24579 S.E. x 24876	47	12	3.9	62.1	Rrrr x RRRr
24583 S.E. x 24856	8	4	2.0	45.9	Rrrr x RRrr
24583 x 24878 (M.P.)[c]	557	145	3.8	64.0	Rrrr x RRRr
24599 S.E. x 24872	8	3	2.7	34.2	Rrrr x RRrr
24638 S.E. x 24830	18	4	4.5	51.6	Rrrr x RRRr
24718 S.E. x 24812	18	5	3.6	69.1	Rrrr x RRRr
24833 S.E. x 24673	835	0	-	-	RRRr x RRRr
24835 S.E. x 24673	762	85	9.0	45.5	RRrr x RRRr
24836 S.E. x 24673	706	0	-	-	RRRR x RRRr
24837 S.E. x 24673	765	0	-	-	RRRr x RRRr
24838 S.E. x 24673	81	0	-	-	RRRR x RRRr
24840 S.E. x 24673	1054	28	38.8	68.2	RRRr x RRRr
24842 S.E. x 24673	252	5	50.4	52.5	RRRr x RRRr
24846 S.E. x 24673	327	3	109.0	24.3	RRRr x RRRr
24849 S.E. x 24670	365	3	121.7	5.3	RRRr x RRrr
24851 S.E. x 24670	425	23	18.5	36.0	RRRr x RRrr
24873 S.E. x 24578	27	4	6.8	31.3	RRRr x Rrrr
24880 S.E. x 24660	267	68	3.9	62.1	RRRr x Rrrr
24884 S.E. x 22709	19	2	9.5	21.4	RRRr x Rrrr

[a] Average percent transmission of homozygous recessive gametes (rr) in both seed and pollen parents estimated from observed ratios.

[b] Plants underlined were rolled as a seedling.

[c] Mutual pollination.

population (table 4). No trends of segregation ratios can be determined from BC_1 data because of the assumed different genetic constitution among F_1 plants and differential transmission rate of homozygous recessive gametes (T-rr rate) between seed and pollen parents in each cross.

Segregation in Self of BC_1 Families

Table 11 and 12 present segregation data from selfs of two BC_1 families. A mutant was used as a seed parent and as a pollen parent in obtaining data shown in tables 11 and 12, respectively. Two of 40 BC_1 plants did not segregate for the rolled-leaf character. All others segregated in the R/r ratios ranging from 0.3 to 340.5 : 1.

Segregation in Crosses between #22448 and Mutant or F_1

Table 13 presents segregation data in crosses between #22448 and several mutant or F_1 plants. The mutants were S_1 plants of #22448. Estimated AT-rr rates are given, along with genotypes proposed. When #22448 was crossed with mutant plants, the R/r ratios ranged from 3.4 to 3.8 : 1. When #22448 was crossed with F_1 plants presumed triplex heterozygotes, the R/r ratios ranged from 16.1 to 71.0 : 1.

Table 11. Segregation of BC_1 (first backcross plants) derived from a cross between #24583 and #24878.

BC_1	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
27125	24583 x 24878	888	129	6.9	2.4	RRrr
27126	"	516	15	34.4	26.4	RRRr
27127	"	1032	115	9.0	2.4	RRrr
27129	"	1719	394	4.4	2.4	RRrr
27130	"	163	1	163.0	26.4	RRRr
27131	"	526	0	-	-	RRRR
27132	"	6	2	3.0	2.4	RRrr
27134	"	242	27	9.0	2.4	RRrr
27135	"	732	22	33.3	26.4	RRRr
27136	"	87	4	21.8	2.4	RRrr
27137	"	680	29	23.4	2.4	RRrr
27138	"	132	3	44.0	26.4	RRRr
27139	"	17	2	8.5	2.4	RRrr
27140	"	356	13	27.4	26.4	RRRr
27141	"	567	11	51.5	26.4	RRRr
27142	"	470	29	16.2	2.4	RRrr
27144	"	350	11	31.8	26.4	RRRr
27145	"	511	2	255.5	26.4	RRRr
27147	"	681	2	340.5	26.4	RRRr
27148	"	208	4	52.0	26.4	RRRr
27149	"	139	2	69.5	26.4	RRRr

[a] Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

Table 12. Segregation of BC_1 (first backcross plants) derived from a cross between #24880 and #24660.

BC_1	Origin	Observed			Expected[a] R/r Ratio	Proposed Genotype
		Normal(R)	Rolled(r)	R/r		
26016[b]	24880 x 24660	312	39	8.0	2.4	RRrr
26017	"	231	3	77.0	26.4	RRRr
26018	"	435	0	-	-	RRRR
26019	"	102	9	11.3	2.4	RRrr
26022	"	866	59	14.7	2.4	RRrr
26023	"	155	2	77.5	26.4	RRRr
26024	"	273	8	34.1	26.4	RRRr
26025	"	8	1	8.0	2.4	RRrr
26026	"	454	14	32.4	26.4	RRRr
26028	"	10	18	0.6	0.3	Rrrr
26029	"	335	23	14.6	2.4	RRrr
26032	"	459	15	30.6	26.4	RRRr
26033	"	54	1	54.0	26.4	RRRr
26035	"	212	2	106.0	26.4	RRRr
26036	"	95	14	6.8	2.4	RRrr
26037	"	627	179	3.5	2.4	RRrr
26038	"	113	2	56.5	26.4	RRRr
26039	"	382	74	5.2	2.4	RRrr
26042	"	130	8	16.3	2.4	RRrr

[a]Expected phenotypic ratios of normal (R) to mutant (r), assuming the maximum frequency of double reductional gametes, complete transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression. Values represent the number of normals divided by mutants.

[b]Plants underlined were rolled as a seedling.

Table 13. Segregation in crosses between #22448 and mutant or F_1 plants.

Cross	Observed			% rr[a] Gamete	Genotype
	Normal(R)	Rolled(r)	R/r		
22448 S.E. x 22603[b]	27	8	3.4	29.3	RRrr x Rrrr
24585 S.E. x 22448	47	13	3.6	25.5	Rrrr x RRrr
24654 x 22448 (M.P.)[c]	151	40	3.8	24.2	Rrrr x RRrr
22448 S.E. x 24854	140	7	20.0	33.2	RRrr x RRRr
24815 S.E. x 22448	213	3	71.0	20.8	RRRr x RRrr
24828 S.E. x 22448	56	3	18.7	35.6	RRRr x RRrr
24830 S.E. x 22448	189	10	18.9	35.2	RRRr x RRrr
24879 S.E. x 22448	450	28	16.1	41.5	RRRr x RRrr

[a] Average percent transmission of homozygous recessive gametes (rr) in both seed and pollen parents estimated from observed ratios.

[b] Plants underlined were rolled as a seedling.

[c] Mutual pollination.

Reciprocal Differences in the R/r Ratio

Table 14 presents the segregation ratio for the rolled-leaf character in the reciprocal crosses. Substantial differences in the R/r ratio were observed between the reciprocal crosses.

Variation in the Rolled-leaf Character

Table 15 presents the rating of the variation of the rolled-leaf character. The relative frequencies are given in the parentheses when the frequency of the extreme mutant was taken as one. No trends were observed in the proportions of different classes. Plant #26864 and #27023 did not segregate for the intermediates. All mutants from the above two plants exhibited the extreme rolled character. In some families, all mutants were slightly rolled. This morphological deformity in other species of grasses was known to exhibit the extreme variability (1, 7, 11, 21, 23). It was assumed that this variation might have been caused by the interaction between rolled-leaf character and other genetic factors affecting leaf shape, such as thickness, width, and length of leaf blade. Variation in expression was also observed among leaves within a culm, among tillers within a plant, and among stages of growth. Thus, it was

Table 14. Comparison of segregation for the rolled-leaf character between reciprocal crosses.

Cross	Observed			% rr[a] Gamete	Genotype
	Normal(R)	Rolled(r)	R/r		
22448 S.E. x 24854[b]	140	7	20.0	33.2	RRrr x RRRr
24854 S.E. x 22448	44	1	44.0	14.9	RRRr x RRrr
22448 S.E. x 24882	114	14	8.1	85.5	RRrr x RRRr
24882 S.E. x 22448	301	17	17.7	37.7	RRRr x RRrr
24599 S.E. x 24856	51	48	1.1	85.6	Rrrr x RRrr
24856 S.E. x 24599	17	9	1.9	48.3	RRrr x Rrrr
24660 S.E. x 24880	26	4	6.5	33.0	Rrrr x RRRr
24880 S.E. x 24660	28	2	14.0	14.0	RRRr x Rrrr

[a] Average percent transmission of homozygous recessive gametes (rr) in both seed and pollen parents estimated from observed ratios.

[b] Plants underlined were rolled as a seedling.

Table 15. Ratings for variation in the rolled-leaf character from selfed progenies.

Plant	Origin	Normal(R)	Rolled(r)[a] A	B	C	D	Total	R/r
22448	1624 x 9723	3838	319	102	168	245	834	4.6
		(12.0)[b]	(1.0)	(0.3)	(0.5)	(0.8)	(2.6)	
22709	22448 ⊗	50	51	25	36	90	202	0.3
		(1.0)	(1.0)	(0.5)	(0.7)	(1.8)	(4.0)	
24660	"	27	10	7	11	38	66	0.4
		(2.7)	(1.0)	(7.0)	(1.1)	(3.8)	(6.6)	
24670	"	1075	56	12	23	45	146	7.4
		(19.2)	(1.0)	(0.2)	(0.4)	(0.8)	(2.6)	
26713	24873 x 24876	277	13	5	5	4	27	10.3
		(21.3)	(1.0)	(0.4)	(0.4)	(0.3)	(2.1)	
26747	"	356	3	3	3	9	15	23.7
		(118.7)	(1.0)	(1.0)	(1.0)	(3.0)	(5.0)	
26864	24876 x 24873	544	181	0	0	0	181	3.8
		(3.0)	(1.0)	(0.0)	(0.0)	(0.0)	(1.0)	
26893	"	329	0	0	0	5	5	65.8
		-	-	-	-	-	-	
26962	22448 ⊗	770	0	0	8	0	8	96.3
		-	-	-	-	-	-	
26965	"	1054	36	12	32	36	116	9.1
		(29.3)	(1.0)	(0.3)	(0.9)	(1.0)	(3.2)	
26976	"	114	0	0	0	14	14	8.1
		-	-	-	-	-	-	
26991		435	15	45	5	5	70	6.2
		(29.0)	(1.0)	(3.0)	(0.3)	(0.3)	(4.7)	
27023	"	520	109	0	0	0	109	4.8
		(4.8)	(1.0)	(0.0)	(0.0)	(0.0)	(1.0)	
27030	"	679	26	10	7	50	93	7.3
		(26.1)	(1.0)	(0.4)	(0.3)	(1.9)	(3.6)	

[a] Rolled-A is for the extremes, rolled-B for those between rolled-A and rolled-C, rolled-C for the intermediates, and rolled-D for the least rolled mutant plants.

[b] Numbers in parentheses are the ratios when rolled-A was taken as 1.0.

assumed that the balance among the factors conditioning leaf shape such as relative growth rate between upper and lower epidermis, might be important in determining the extent of leaf rolling.

Cytology

Somatic chromosome numbers were determined for 44 mutant and 41 F_1 plants. A chromosome number of 56 was predominant, although plants with 52, 53, 54, 55, and 57 chromosomes were observed. Mutants #24634 and #24655 had 51 and 52 chromosomes, respectively, and survived for 5 months. It was concluded that mutant plants normally had 56 chromosomes, and that the rolled-leaf character was caused by a gene mutation rather than aneuploidy.

DISCUSSION

The Proposed Mode of Inheritance

Numerous earlier geneticists encountered "mysterious" inheritance patterns in several polyploid species. Stanford (35) reported, in his study on inheritance of purple flower in alfalfa, that most of the F_1 plants were different in genetic constitution. He suggested tetrasomic inheritance but could not exclude disomic inheritance. He also mentioned the importance of F_3 data in genetic studies on tetrasomic inheritance. Nielsen (31) observed a continuous series of segregation ratios ranging from 4.6 to 572 : 1 for green versus chlorophyll-deficient mutant plants in timothy. He suggested several possible explanations for the divergent ratios, such as preferential pairing, selective fertilization, differential lethality among gametes. No experimental data were presented for the above explanations. Van Dijk (36) observed the following from an inheritance study of harsh leaves in tetraploid cocksfoot; 1) surplus of recessives in some families, 2) the occurrence of rare segregants, 3) reciprocal differences in segregation ratios. In most cases, he could explain his data by assuming one

dominant factor supplemented by minor genes. Other possible explanations offered were the existence of complementary factors and a system of more factors with incomplete dominance.

All of the segregation patterns described above were exhibited in the present study on the rolled-leaf mutant in smooth bromegrass. These results showed a wide range of segregation ratios in the F_2 and a deficiency of the assumed duplex class in F_1 populations (table 4), indicating a heterogeneity of the supposedly homogeneous F_1 population, and a deficiency of homozygous recessive gametes from mutant plants. Almost continuous segregation ratios were observed ranging from 6.5 : 1 to no segregation from the same presumed genotype, indicating the existence of an environmental influence or interaction among unknown factors affecting the occurrence of recessives (table 4). Surplus recessives were observed in the segregation of #22448 (table 2), perhaps indicating the existence of incomplete dominance. The occurrence of such rare segregants as #24841 and #24849 (table 4), and #25762 (table 7) indicates considerable number of double reductional gametes. Reciprocal differences in segregation ratios (table 14) suggest that there may be a differential effect of the rolled-leaf

mutant on reproductive function of the pollen and seed parent. Variable expression of the rolled-leaf character among the mutants themselves (table 15) indicates that the expression of the trait may be controlled not only by the rolled-leaf gene with modifiers but also by interaction among several other segregating factors.

From evidence presented in this study and reported in the literature, the following proposal is made for the rolled-leaf mutant in Bromus inermis. The scheme is a simple tetrasomic inheritance modified by 1) differential transmission of homozygous recessive gametes (rr) between seed and pollen parents and 2) incomplete dominance requiring at least two doses of the dominant allele to suppress expression of the recessive.

The following assumptions were made in testing the observed data.

1. A single factor tetrasomic inheritance.
2. Incomplete dominance requiring at least two doses of the dominant allele to suppress mutant expression. Phenotypically mutant plants would be genotypically simplex (Rrrr) or nulliplex (rrrr) plants. Normal plants would be genotypically quadruplex (RRRR), triplex (RRRr) or duplex (RRrr) plants.

There are three genotypic classes in the normal phenotypes and two in the mutant.

3. The maximum value of α (α = 1/6) was employed in calculations of the expected phenotypic ratios. Therefore, the frequency of homozygous gametes, RR and rr, would be biased upward somewhat.
4. Differential transmission of homozygous recessive gametes between seed and pollen parents.

Calculation of Expected Phenotypic Ratios

The procedure can be explained below with an example by selfing of a duplex plant. Table 16 illustrates the gametic and zygotic frequencies from the self of a duplex individual, assuming α = 1/6, and differential transmission rate of homo-recessive gametes (T-rr rate) of 100%, 50%, and x%.

The genotypic ratio of zygotes is 4RRRR : 20RRRr : 33RRrr : 20Rrrr : 4rrrr, when T-rr rate is 100%. The phenotypic ratio is (4RRRR + 20RRRr + 33RRrr)R : (20Rrrr + 4rrrr)r, or 57R : 24r, or an R/r ratio is 2.4 : 1. Following the above method, the minimum limits of the expected R/r ratios were calculated for selfs and crosses of various genotypes (table 17). Since ratios in table 17 are the extreme cases, the actual ratios would be greater than

Table 16. Diagramatic illustration of gametic and zygotic frequencies from the self of a duplex plant, assuming α = 1/6, and 100, 50 and x% T-rr rates.

Female Gam. Freq. & T-rr Rate		Male Gam. Freq. 2RR	5Rr	T-rr Rate 100% 2rr	50% 1rr	x% (2x)rr
	2RR	4RRRR	10RRRr	4RRrr	2RRrr	(4x)RRrr
	5Rr	10RRRr	25RRrr	10Rrrr	5Rrrr	(10x)Rrrr
T-rr Rate 100%	2rr	4RRrr	10Rrrr	4rrrr	2rrrr	(4x)rrrr
50%	1rr	2RRrr	5Rrrr	2rrrr	1rrrr	(2x)rrrr
x%	(2x)rr	(4x)RRrr	(10x)Rrrr	(4x)rrrr	(2x)rrrr	$(4x^2)$rrrr

Table 17. Minimum limit of the expected phenotypic ratio (R/r) in selfs and crosses for the rolled-leaf character, assuming a simple tetrasomic gene with α = 1/6, 100% transmission of homozygous recessive gametes (rr), and incomplete dominance requiring at least two dominant alleles to suppress mutant expression.

Seed Parent	Pollen Parent				
	RRRR	RRRr	RRrr	Rrrr	rrrr
RRRR	-[a]	-	-	-	-
RRRr	-	26.4	7.0	2.8	1.2
RRrr	-	7.0	2.4	0.9	0.3
Rrrr	-	2.8	0.9	0.3	0.04
rrrr	-	1.2	0.3	0.04	-

[a] Ratios underlined indicate selfs.

shown. There are two factors involved in determining R/r ratios. First, as α departs from the maximum value, 1/6, the relative frequency of RRrr will be increased, thus decreasing the frequency of Rrrr and rrrr, or increasing the R/r ratio. Second, as T-rr rate departs from the maximum 100%, the relative frequency of RRrr, Rrrr and rrrr will be decreased, while the frequency of RRRR and RRRr remains the same.

A generalized formula can be derived for the phenotypic R/r ratios, with a variable T-rr rate, x. For the sake of simplicity, the same T-rr rate between seed and pollen parents, or average T-rr rate (AT-rr rate) will be assumed. From table 16, the frequency of normal plants will be RRRR + RRRr + RRrr, or 4 + 20 + 25 + 4x + 4x, and the frequency of mutant plants will be Rrrr + rrrr, or 10x + 10x + $4x^2$. Therefore, the R/r ratio will be $(49 + 8x)R : (20x + 4x^2)r$. If the AT-rr rate is 50%, the R/r ratio will be $(49 + 8(.5))R : (20(.5) + 4(.5)^2)r$, or 53R : 11r, or an R/r ratio of 4.8 : 1. A general formula for phenotypic ratios with AT-rr rate, x%, in selfing of a duplex, is "$R/r = (49 + 8x)/(20x + 4x^2)$". It is obvious from the above formula that the phenotypic ratio (R/r ratio) is a function of AT-rr rate, x, whose effect is greater on the frequency of recessives. Similarly, general formulae can

be derived for selfs or crosses for all genotypes and genotypic combinations.

If the AT-rr rate is 0, or no transmission of rr gametes through either parent, no Rrrr or rrrr progenies will be produced irrespective of the genotypes. That is, any genotype can result in a non-segregant for the rolled-leaf character in extreme cases. If the AT-rr rate is very small, as it most likely is in a triplex, mutant segregants will be rare and the R/r ratio will be high, resulting in the rare segregant.

Proposed Genotypes

The proposed genotypes in tables 2 through 9, 11, and 12 were established according to the following scheme. Because the exact value of T-rr rate is unknown and variable as indicated by differences in the R/r ratios between years (table 3), the maximum likelihood interpretation seems most reasonable. For the inbred populations, if the observed R/r ratio was higher than 26.4 (table 17), it was proposed to be a triplex. If the ratio fell between 2.4 and 26.4, it was proposed to be a duplex. If the ratio was lower than 2.4, it was proposed to be a simplex. If the plant did not segregate for rolled or normal, it was proposed to be quadruplex or nulliplex, respectively. If the

R/r ratio was about 2.5 or 2.8 : 1 but the phenotype was rolled, they were still proposed to be simplex, as can be seen for #26092 and #26094 in table 3.

Calculation of Estimated AT-rr Rate

Although differential T-rr rate was indicated between pollen and seed parents, for the sake of simplicity, the average T-rr rate (AT-rr rate) was estimated based on the observed ratio and proposed genotypes of seed and pollen parents (tables 10, 13, and 14). The procedure can be described through an example illustrating how an R/r ratio of 20.0 : 1 might have occurred in a cross, #22448 x #24854 (table 13). The genotype of #22448 was proposed to be RRrr based on the segregation data in table 2. The genotype of the F_1, #24854, was proposed to be RRRr based on the F_2 segregation ratio (table 4). Let x be the AT-rr rate and f be the observed R/r ratio. The zygotic outcome from the above cross would be :

Female Gamete	Male Gamete 13RR	10Rr	(x)rr
2RR	26RRRR	20RRRr	(2x)RRrr
5Rr	65RRRr	50RRrr	(5x)Rrrr
(2x)rr	(26x)RRrr	(20x)Rrrr	($2x^2$)rrrr

The phenotypic ratio will be, (RRRR + RRRr + RRrr)R : (Rrrr + rrrr)r. We can derive a quadratic equation from the derived R/r ratio and the observed ratio, f.

$$(26 + 85 + 50 + 2x + 26x) : (5x + 20x + 2x^2) = f : 1$$

$$(161 + 28x) = (25x + 2x^2)f$$

Replace f with observed ratio, 20.0.

$$(161 + 28x) = (25x + 2x^2)(20)$$

$$x^2 + 11.8x - 4.025 = 0$$

The x can be solved by a simple solution of a quadratic equation as follows:

for $ax^2 + bx + c = 0$

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

therefore,

$$x = \frac{-(11.8) \pm \sqrt{(11.8)^2 - (4)(1)(-4.025)}}{(2)(1)}$$

$$x = 0.332, \text{ or } -12.132$$

$$\therefore x = 0.332, \text{ or } 33.2\%$$

With a 100% AT-rr rate, the expected R/r ratio is 7.0 for a cross of RRrr x RRRr, as shown in table 17. The observed R/r ratio of 20.0 : 1 would be expected if there were 33.2% AT-rr rate in a cross, #22448 x #24854.

Differential T-rr Rates between Seed and Pollen Parents

The transmission rate of homozygous recessive gametes (T-rr rate) may be not only a property of a genotype but also an interaction between genotypes. When #22448 was used as a common pollen source, AT-rr rates ranged from 20.8% to 41.5%, indicating a considerable variation in the T-rr rate among seed parents (table 13).

In table 14, estimated AT-rr rates dropped to about one half whenever genotypes with more recessive alleles were used as a pollen parent in the reciprocal crosses. The AT-rr rates became different in the reciprocal crosses because the AT-rr rates were based on different observed R/r ratios. Thus, a differential T-rr rate between seed and pollen parents was postulated. If the T-rr rate is the in both parents and if the same genotypes are involved in a cross, there would be no reciprocal differences, as shown in tables 17 and 18.

In the earlier discussion on calculation of estimated AT-rr rate, it has been noted that only the zygotic frequencies of RRrr, Rrrr, and rrrr are influenced by incomplete AT-rr rates. When the T-rr rate and genotypes of seed and pollen parents are different, only the frequencies of RRrr and Rrrr genotypes are influenced between the

Table 18. Effect of differential T-rr rates in seed and pollen parents on reciprocal differences in the cross, RRRr x Rrrr, assuming a constant AT-rr rate of 40%.

% T-rr rate in		Cross		
Female	Male	RRRr x Rrrr	Rrrr x RRRr	Ratio[a]
70	10	12.2[b]	4.0[b]	3.1
60	20	8.6	4.3	2.0
50	30	6.6	4.8	1.4
40	40	5.5	5.5	1.0
30	50	4.7	5.9	0.8

[a] Values represent the ratio of reciprocal phenotypic ratios from the cross, RRRr x Rrrr.

[b] Phenotypic ratios of normal (R) to mutant (r) with corresponding % T-rr rates.

reciprocal crosses. The frequencies of RRRR, RRRr, and rrrr genotypes remain the same irrespective of the direction of cross, as shown in table 19. If the T-rr rate were lower in the pollen parent than in the seed parent, the proportion of the decreased rr-gamete would be greater when a genotype with more recessive alleles was used as a pollen parent, producing a reduced number of RRrr and Rrrr genotypes (table 19). If Rrrr were pollen parent and RRrr the seed parent, the rate of decreased RRrr and Rrrr progenies would be greater resulting in a higher R/r ratio than if Rrrr were the seed parent.

Table 18 shows the effect of differential T-rr rates in seed and pollen parents on reciprocal differences in the cross, RRRr x Rrrr, assuming a constant AT-rr rate of 40%. The average AT-rr rate of 40% was based on data from 32 crosses which were listed in tables 10, 13, and 14. There are no reciprocal differences when the T-rr rates are the same in both parents. When the AT-rr rate is kept constant at 40%, the ratios of reciprocal phenotypic ratios increase as the T-rr rates in the seed parent increase. Differential T-rr rates of 60% and 20% for seed and pollen parents, respectively, were the closest approximation to the observed reciprocal differences.

Table 19. Expected genotypic ratios for the rolled-leaf character among progenies derived from selfs or crosses, assuming a simple tetrasomic gene with α = 1/6, and T-rr rates of 60% and 20% in seed and pollen parents, respectively.

Parental Genotype	Phenotype							
	Normal(R)				Rolled(r)			
	RRRR	RRRr	RRrr	Total[a]	Rrrr	rrrr	Total[a]	R/r
RRRr x RRRr or RRRr ⊗	169.0	260.0	110.1	(539.1)	8.0	0.1	(8.1)	66.6
RRrr x RRrr or RRrr ⊗	4.0	20.0	28.2	(52.2)	8.0	0.5	(8.5)	6.1
Rrrr x Rrrr or Rrrr ⊗	1.0	20.0	110.4	(131.4)	104.0	20.3	(124.3)	1.1
RRRR x RRRr	13.0	10.0	0.2	(23.2)	-	-	-	-
RRRr x RRRR	13.0	10.0	0.6	(23.6)	-	-	-	-
RRRR x RRrr	2.0	5.0	0.4	(7.4)	-	-	-	-
RRrr x RRRR	2.0	5.0	1.2	(8.2)	-	-	-	-
RRRR x Rrrr	1.0	10.0	2.6	(13.6)	-	-	-	-
Rrrr x RRRR	1.0	10.0	7.8	(17.8)	-	-	-	-
RRRr x RRrr	26.0	85.0	56.4	(167.4)	7.0	0.2	(7.2)	24.2
RRrr x RRRr	26.0	85.0	66.6	(177.6)	13.0	0.2	(13.2)	13.5
RRRr x Rrrr	13.0	140.0	134.4	(287.4)	32.0	1.6	(33.6)	8.6
Rrrr x RRRr	13.0	140.0	201.6	(354.6)	80.0	1.6	(81.6)	4.3
RRrr x Rrrr	2.0	25.0	56.4	(83.4)	25.0	3.1	(28.1)	3.0
Rrrr x RRrr	2.0	25.0	66.0	(93.0)	43.0	3.1	(46.1)	2.0

[a] Figures in parentheses represent a total of genotypes within each phenotypic class.

Table 19 presents expected genotypic ratios in selfs or crosses for various genotypes, which were calculated according to differential T-rr rates of 60% and 20% for seed and pollen parents, respectively. These expected genotypic ratios were used in testing observed genotypic ratios in F_2 and other families in tables 2, 3, 5 through 9, 11, and 12.

Another possible explanation for differences in reciprocal crosses would be complementary effects between several factors, as postulated by Van Dijk (36). A plant might behave as a simplex, and sometimes as a duplex in different crosses, depending upon the alleles at the other loci which interact with the locus in question. Such possibilities were not satisfactory for the observed ratios from the present study.

Test of Observed Ratios

The test of observed ratios against expected ratios derived from the proposed mode of inheritance, was concentrated on observed genotypic ratios rather than phenotypic ratios. Phenotypic ratios were not tested but subjected to the maximum likelihood interpretation. Table 20 presents the results of X^2-test of observed genotypic ratios from 8 segregating families from S_1 populations of #22448, F_2,

Table 20. Chi-square test of observed genotypic ratios in the S_1 of #22448, F_2 and BC_1 families against expected genotypic ratios which were presented in table 19.

Family	Origin	Genotype[a]		Genotypic Frequency RRRR	RRRr	RRrr	X^2	P.(df = 2)	From Table
S_1	22448 ⊗	RRrr	obs.	4	26	54			
			exp.	6.5	32.0	45.5	3.68	.10 - .20	2,3
F_2	24811 ⊗	RRRr	obs.	10	17	8			
			exp.	10.7	17.2	7.1	0.16	.90 - .95	5
F_2	24866 ⊗	RRRr	obs.	21	41	15			
			exp.	23.6	37.7	15.7	0.61	.70 - .90	6
F_2	24835 x 24837	RRrr x RRRr	obs.	10	36	21			
			exp.	9.7	32.0	25.3	1.24	.50 - .70	7
F_2	24846 x 24833	RRRr x RRRr	obs.	17	27	16			
			exp.	18.4	29.4	12.2	1.49	.30 - .50	8
F_2	24876 x 24873	RRRr x RRRr	obs.	23	40	21			
			exp.	25.7	41.2	17.1	1.21	.50 - .70	9
BC_1	24583 x 24878	Rrrr x RRRr	obs.	1	11	9			
			exp.	0.8	8.3	11.9	1.61	.30 - .50	11
BC_1	24880 x 24660	RRRr x Rrrr	obs.	1	8	9			
			exp.	0.7	7.3	10.0	0.30	.70 - .90	12

[a]Proposed genotype of origin.

and BC_1 populations (tables 2, 3, 5 through 9, 11, and 12) against expected ratios in table 19. Plant #22448 segregated in an R/r ratio of 4.6 : 1 and was assumed to be a duplex plant (table 2). A total of 365 S_1 plants were planted. Only 98 plants produced enough S_2 seeds to be used in the analysis (tables 2 and 3). Fourteen Rrrr and rrrr genotypes were excluded from the test because of their low fertility. Only the numbers of RRRR, RRRr and RRrr genotypes were subjected to the X^2-test. The observed genotypic ratio from the S_1 populations of #22448 barely fit the expected ratio (table 20).

A total of 407 F_2 plants was used to determine the genotypic ratios in F_2 families. The F_1, #24811, was assumed to be a triplex, based on the F_2 segregation ratio. According to the proposed scheme, the genetic constitution of this F_2 family should approach 169RRRR : 260RRRr : 110.1RRrr, or 1.5RRRR : 2.4RRRr : 1.0RRrr (table 19). The F_2 plants derived from the F_1, #24811, segregated in the genotypic ratio of 10RRRR : 17RRRr : 8RRrr, or 1.3RRRR : 2.1RRRr : 1.0RRrr (table 5). The probability was high (P. = .90) that the deviation of this ratio from the expected was due to chance. Therefore, the observed ratio fit the expected ratios. Genotypic ratios in 4 other F_2 families and 2 BC_1

families were in good to fair agreement with the expected ratios. Thus, the proposed mode of inheritance was supported.

The Factor α

The factor α could not be explored readily in this study. The minor effect of α on the genotypic frequency was hidden by the major effect of T-rr rate. Because α was assumed to be the maximum value of 1/6, the estimated frequency of RRRR tended to be higher than the actual. The factor, α , could possibly be calculated if there were sufficient fertility in simplex plants. The frequency of RRRR from the segregation of simplex would be a direct indication of double reductional gametes. The frequency of RRrr would be disturbed by the variable T-rr rate. The genotypes, Rrrr and rrrr, would not produce enough seeds. Therefore, the genotypic ratios of RRRR and RRRr would be the only ones available for the test of goodness-of-fit.

Other Possible Explanations Considered

Several explanations were also considered. Preferential pairing was ruled out as one of the possible explanations for the rare segregant in the present study. The F_1, #24866, segregated in an R/r ratio of 241.0 : 1 in

1976 (table 4, section 1). From the same F_2 population, the normal plants were chosen at random to be planted to obtain F_3 seeds. The genotypic ratio of RRRR, RRRr and RRrr would have to, accordingly, be altered to give the high ratio of 241.0 : 1 by incomplete preferential pairing. The genotypic ratio in F_2 fit the expected ratios from the proposed scheme of inheritance with P. = .70 - .90. Therefore, preferential pairing does not appear to be a proper explanation for the rare segregant in the present study.

The scheme of disomic, hexasomic, and octosomic inheritance could not explain the concurrent occurrence of the rare segregants and the surplus recessives within a family. Complementary effects of two or more factors with incomplete dominance, and a polygenic system with a threshold effect were not satisfactory to explain the surplus recessives and reciprocal differences in segregation ratios. Dosage effect or interaction between a cytoplasmic gene or genes and nuclear gene or genes were not indicated by the data. The cytological analysis contributed little toward a solution of the problem, as Stanford had mentioned (35).

Difficulties in Interpretation

Although the observed genetic data supported the proposed mode of inheritance of the rolled-leaf mutant in

smooth bromegrass, the conclusion is still based on several unconfirmed hypotheses. Derived figures against which the observed ratios were tested were only a close approximation to the facts. There were apparent sources of error other than experimental error. The maximum value of α was used only for the sake of simplicity in the calculation. Considering the presumed great variations in the T-rr rates, it seems oversimplified to assume a T-rr rate of 60% and 20% for all seed and pollen parents, respectively. The variable expression of the mutant character often made scoring difficult during the early period of the study, which led to loss of some potential data. Correlations between occurrence of the mutant and self-fertility may totally upset the proposed scheme. The wide range of variation in the segregation ratios between years on the same plant could not be overlooked as a possible source of error. A large number of progenies may be required over several years to identify the genotype. The variable nature of segregation leads one to be conservative in assigning a genotype to each plant.

Genetic evidence alone without support by cytological or biochemical investigations may not be sufficient for determining the precise mode of inheritance. Differential transmission of rr-gamete was indicated by reciprocal

differences in the segregation ratio. Other studies may be needed. The key to understanding this problem may relate to gametogenesis or fertilization. There may be an abnormality during meiosis, or there may be pollen competition between different genotypes. There may be linkage between the gene "r" and genes governing the incompatability system. Whatever the cause, Bromus inermis seems to have a genetic system that tolerates and gradually eliminates harmful off-types from the species.

CONCLUSION

Inheritance of a rolled-leaf mutant in smooth bromegrass, Bromus inermis Leyss., was investigated. The data presented support a mode of a simple tetrasomic inheritance with differential transmission of the homozygous recessive gametes between seed and pollen parents, and incomplete dominance requiring at least two dominant alleles to suppress expression of the recessive. The incompletely dominant normal allele of the rolled-leaf gene was represented by the symbol "R", and the recessive mutant allele by the symbol "r". Therefore, a phenotypically rolled-leaf plant would be Rrrr or rrrr, and a phenotypically normal plant would be RRRR, RRRr, or RRrr. Possible explanations were presented for the rare segregant, surplus recessives, and reciprocal differences in segregation ratios.

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